

# **Ecology of Honeyeaters (Meliphagidae) in Western Australian Eucalypt Woodlands I: Resource Allocation Among Species in the Great Western Woodland During Spring**

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## **ABSTRACT**

Nectar-feeding birds are commonly the most abundant birds in Australian eucalypt forests and woodlands, where they play a key role as pollinators of native plants. Among the nectar-feeders, honeyeaters (Meliphagidae) are particularly aggressive and may exclude other birds from the habitats they occupy thereby affecting the composition of avian communities and the distribution of species on a landscape scale. Such behaviour has cascading effects on ecosystems, changing the abundances and kinds of plant-eating arthropods. A comprehensive knowledge of the ecology of honeyeaters is therefore basic to the conservation management of Australia's natural environments. In this paper, we describe the foraging ecology of honeyeaters in the Great Western Woodland (GWW) during the spring, comparing the use of resources between species and locations. Species of honeyeaters in the GWW differ morphologically, and in social and dispersive behaviour, but aggregate in multi-species flocks on blossoming eucalypts (*Eucalyptus* spp.), the main source of nectar. There are differences among the species of honeyeaters in the eucalypts frequented as nectar sources, with these differences reflecting differences among species in habitat. Species also differ in foraging manoeuvres (the way food is taken), substrates, and heights, as well as the plant species visited when feeding on foods other than nectar (e.g., lerp, arthropods, and fruit). The use of substrates and foraging manoeuvres differed between locations. Differences in foraging ecology between locations were primarily related to differences in flowering phenology and vegetation structure (e.g., height, type of bark) and floristics, which in turn affected the food resources available to honeyeaters. Our observations support arguments that the long-term conservation of nectar-feeders cannot be achieved by relying on a fragmented system of widely dispersed conservation reserves. This is especially true in an era of accelerated climate change. Instead, a landscape scale, if not a continental scale, approach to ecosystem conservation that emphasizes habitat connectivity is required.

**Key words:** foraging ecology, Great Western Woodland, habitat fragmentation, honeyeater, Meliphagidae, nectar-feeders, nomadic birds, resource partitioning

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## **Introduction**

Nectar-feeding birds are commonly the most abundant birds in Australian eucalypt forests and woodlands (Keast 1968, 1985; Ford and Paton 1977; Ford 1989) and play a key role as pollinators of native plants (Keast 1968; Pyke 1980; Recher 1981). In addition, some species of honeyeaters (Meliphagidae) exclude other birds from the habitats they occupy influencing the composition of avian communities and the distribution of species on a landscape scale (Loyn *et al.* 1983; Grey *et al.* 1998; Wardell-Johnson *et al.* 2005). Such behaviour changes the abundances and kinds of plant-eating arthropods, thereby affecting the health of plants and entire ecosystems (Loyn *et al.* 1983; Grey *et al.* 1998; Wardell-Johnson *et al.* 2005). Aggregations of nectar-feeders in locations of high nectar abundance also affect avian communities by attracting predatory birds (Recher and Davis 2002). Understanding the ecology

of nectar-feeders and their interactions with their food plants and other species of plants and animals is basic to understanding the ecology of Australian ecosystems and how they can be best managed and conserved.

We have studied the ecology of eucalypt forest and woodland nectar-feeders in Western Australia since 1986. Nectar-feeders are abundant in these habitats, commonly aggregating in large, speciose flocks on blooms of nectar-rich flowers (HFR pers obs.). Previously aspects of the foraging ecology of nectar-feeders at Mt Gibson on the northern edge of the West Australian wheatbelt and at Dryandra on the western edge were described by Recher and Davis (2010, 2011) and Wilson and Recher (2001). In this and subsequent papers we present observations on the ecology of nectar-feeders during spring in eucalypt woodlands in the Great Western Woodland (GWW). The

GWW is the largest temperate woodland remaining in southern Australia (Watson *et al.* 2008).

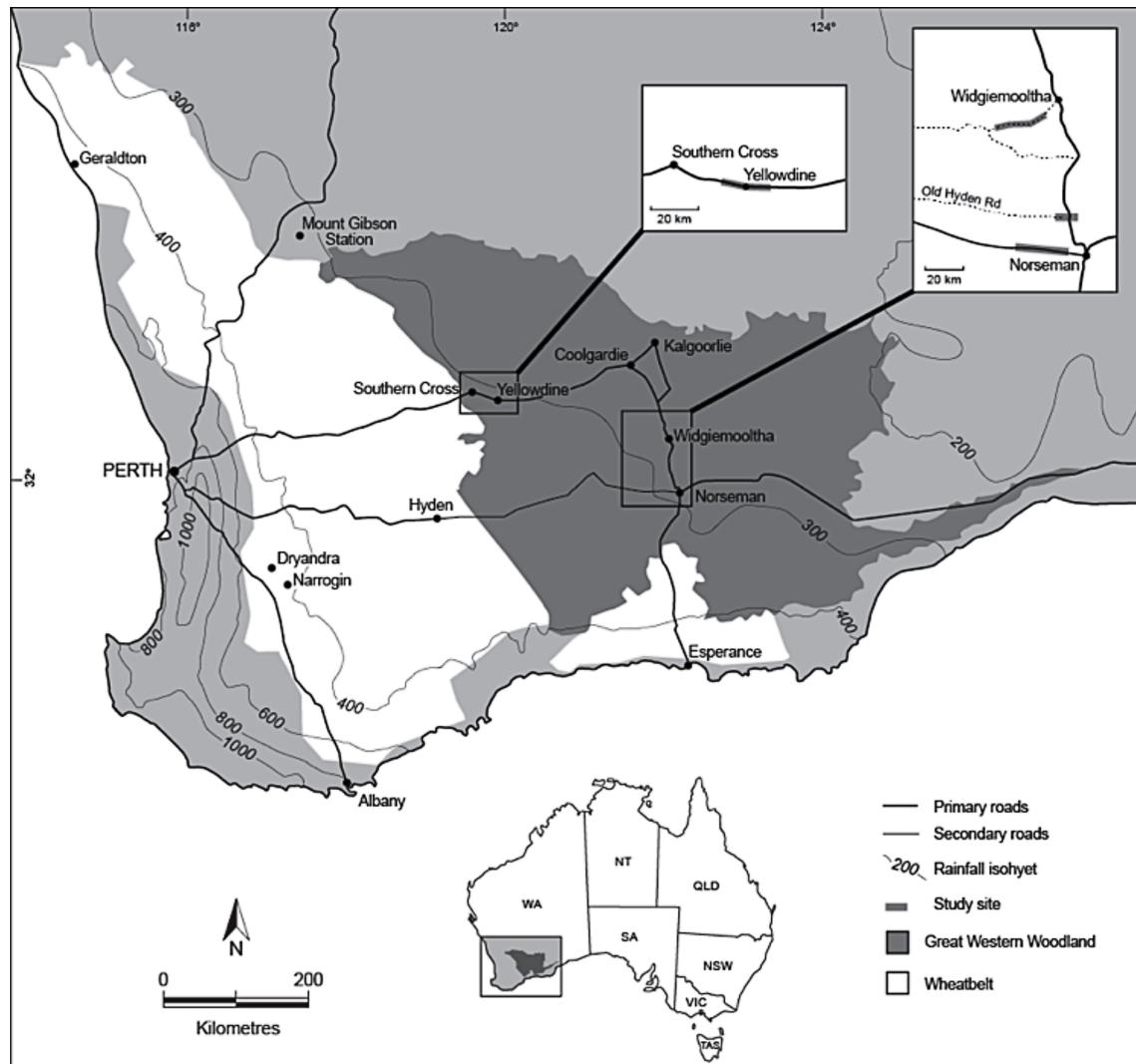
Our objectives are to describe the foraging ecology of honeyeaters in the GWW; the plants visited for nectar, those used when foraging for food other than nectar, the heights at which birds foraged, the foraging manoeuvres used to take food, the substrates on which different food resources were located, and how these differed among species and between different locations within the GWW. We also consider differences between long- and short-billed species, because differences in bill shape and size are reliable predictors of meliphagid foraging ecology (Ford and Paton 1976, 1977, 1982; Mac Nally 1994). These data are useful for a general understanding of meliphagid ecology in the GWW, how co-habiting species allocate resources, and for the generation of hypotheses regarding feeding behaviour, niche structure, and species association to be tested in subsequent papers. Our observations establish a baseline against which change in honeyeater abundances and behaviour over time can be measured and the effects of climate change and other anthropogenic

impacts monitored. The conservation management applications of the data are discussed.

## Study Location

The GWW covers 16–21 million hectares of eucalypt woodland, shrubland, and salt lakes centred on Norseman and Kalgoorlie east of the wheatbelt in Western Australia (Figure 1) (Watson *et al.* 2008). Within the GWW, we had four study locations: Yellowdine east of Southern Cross along the Great Eastern Highway; Widgiemooltha south of Coolgardie on the Coolgardie-Norseman Road; Norseman North on the Coolgardie-Norseman Road north of Norseman; and, Norseman West along the Hyden-Norseman Road west of Norseman (Figure 1). Not every location was sampled in all years, or for the same lengths of time. We studied birds variously from late August to mid-October at Yellowdine in 1997, 2001, 2005–7, and 2010; Widgiemooltha 2005–7; Norseman North 2006–8, 2010; and, Norseman West 2003, 2005–8, 2010.

In each location, we had multiple study sites where we recorded the abundances and foraging behaviour of



**Figure 1.** Map of the Great Western Woodland (GWW) showing locations of principal study areas and sites. The white area representing Western Australia's wheat-sheep belt is predominantly (>90 %) cleared. The grey areas east of the GWW are semi-arid shrublands. Those west of the wheatbelt are dominated by forests and tall, open-woodlands, along with cleared agricultural and residential lands.

all birds encountered. At Yellowdine, twelve sites were located along 20 km of the Great Eastern Highway centred on the Yellowdine Roadhouse ( $31^{\circ} 17'S$ ,  $119^{\circ} 39'E$ ) (359-404 m amsl [above mean sea level]). At Widgiemooltha, 19 sites centred on  $31^{\circ} 36'S$ ,  $121^{\circ} 31'E$  (309-444 m amsl) were sampled in 2005, four of which were along the Binneringie Road east of the Coolgardie-Norseman Road. The Binneringie Road sites were not sampled after 2005. The remaining sites were located along the Cave Hill Road west of Widgiemooltha at intervals of about 5 km according to habitat suitability. At Norseman, 16 sites centred on  $31^{\circ} 57'S$ ,  $121^{\circ} 39'E$  (266-310 m amsl) were located  $\sim 25$  km north of Norseman east and west of the Coolgardie-Norseman Road (Norseman North), with 14 sites along the Hyden-Norseman Road 9 to 40 km west ( $32^{\circ} 11'S$ ,  $121^{\circ} 38'E$  to  $32^{\circ} 01'$ ,  $121^{\circ} 31'E$ ; 311-403 m amsl) of Lake Cowan (Norseman West). Sites were  $\sim 10$  ha in size, irregular in shape according to habitat, and were selected to sample the range of woodland habitats within each location. We did not work on any sites where shrubs or mallees dominated the vegetation.

All sites were open eucalypt woodland, although some sites had canopy cover  $> 40\%$  and could be described as 'forest'. Sites differed among and within locations in canopy cover, canopy height, understorey and shrub vegetation, and plant species composition. Precise quantitative measurements of the vegetation were not made. Instead, we relied on detailed descriptions of the vegetation and estimates of height and cover of the different vegetation layers by HFR, who also identified the species of plants used by honeyeaters. Sites fell within an elevation range of 266 - 444 m amsl, with broad, flat ridges, gentle slopes, and wide, flat run-on areas that received water from the slopes. Drainage was internal and except immediately after rain there was no surface water. Soils were primarily soft calcareous earths, sandy loams, and alluvials, with some laterites on ridge lines (Berry *et al.* 2010; HFR pers obs.). Most sites had a well-developed biocrust (cryptogrammic crust) that hydrated rapidly with rain (see Appendix 1 in Recher and Davis 2014 for photographs of habitats). GPS co-ordinates of all sites are available from HFR.

On all sites the composition and structure of the vegetation changed over short distances with small changes in slope and soil. Eucalypts formed open to closed canopies from 15-30 m in height, with emergents to 40-45 m. The most abundant eucalypts were Dundas Blackbutt *Eucalyptus dundasii*, Gimlet *E. salubris*, Goldfields Blackbutt *E. lesouefii*, Merrit *E. flocktoniae*, Red Morrel *E. longicornis*, Redwood *E. transcontinentalis*, Ribbon Gum *E. sheathiana*, and Salmon Gum *E. salmonophloia*, along with a variety of mallees (*Eucalyptus* spp.), including Sand Mallee *E. eremophila*, Square-fruited Mallee *E. calycogona*, and Yorrell *E. yilgarnensis*. Most mallees could not be identified to species. Understories were discontinuous and variously dominated by young eucalypts and mallees. Shrub layers were rich in species and multi-layered, but patchy in distribution. Where canopies were open, shrubs formed nearly continuous layers from 50 to 600 cm in height. Broom Bush *Melaleuca uncinata* were the tallest shrubs forming dense, patchily distributed, monospecific stands. Shrubs in the genera *Acacia*, *Atriplex*, *Cassia*, *Dodonea*, *Eremophila*, *Exocarpos*,

*Grevillea*, *Mareiana*, *Melaleuca*, and *Persoonia*, among others were abundant. Ground vegetation was mainly ephemeral, comprising low (< 30 cm) forbs and shrubs that included species of *Atriplex*, *Brachycome*, *Maireana*, and *Ptilotus*. Grasses were uncommon. As with the shrub layer, the ground vegetation was patchy and rarely continuous. The result for all sites was a complexly structured canopy, understory, shrub, and ground vegetation, with considerable open space and variation in the composition and height of dominant plants in each vegetation layer. Bare ground was 30 to 80 % of the ground surface, with litter and coarse woody debris, including logs, covering 20 to 70% of the soil surface depending on canopy cover and exposure to wind. Fallen leaves and bark tended to windrow among shrubs, along logs, among woody debris, and at the base of trees. Accumulations of litter and woody debris were, however, sparse, probably because of termite (Isoptera) activity.

The sites at Yellowdine and Widgiemooltha had a history of disturbance by logging, roads, pipelines, and mining exploration commencing in the 19<sup>th</sup> Century. Three sites at Widgiemooltha were dominated by even-aged regeneration following clear-felling in the 1930s or earlier. There was less evidence of disturbance on the Norseman sites, although the woodlands around Norseman also have a long history of logging, road construction, and mining disturbance. Some sites north and west of Norseman were even-aged post-fire regeneration with ages estimated by HFR at 70-150+ years<sup>1</sup>, and most had evidence of selective logging and fuel wood cutting. Four sites north of Norseman were even-aged (30 – 50 years) stands of Merrit and Redwood following wildfire or clear-felling.

## Species Of Honeyeaters

Sufficient data for analysis were obtained for eight species of honeyeaters (Table 1). A ninth species, the Pied Honeyeater *Certhionyx variegatus*, was recorded at Norseman West (2003) and Widgiemooltha (2005), but only 10 observations of birds taking nectar from *Grevillea* sp. at Norseman West were obtained and this species was excluded from analyses.

## Morphology and social behaviour

Of the species analysed, four, Red Wattlebird, and Spiny-cheeked, White-fronted, and Brown Honeyeaters, have long, decurved bills suited for taking nectar from flowers, and following Ford and Paton (1977) are termed 'long-billed' species (Table 1). Four others, Yellow-throated Miner, and White-eared, Yellow-plumed, and Brown-headed Honeyeaters, have short, straight bills suited for taking lerp, manna, honeydew, and arthropods from foliage and bark, and are termed 'short-billed' species (Table 1). Ford and Paton (1977) considered long-billed honeyeaters to be primarily nectarivorous and short-billed honeyeaters to be primarily insectivorous, thereby separating the honeyeaters into two distinct guilds.

There are size differences in each group. Among the

<sup>1</sup> HFR estimated age based on extensive experience (1968-2010) with known age post-fire and logging regeneration in eucalypt woodlands and forests in eastern and western Australia, including the GWW.

**Table 1.** Morphological characteristics of honeyeaters (Meliphagidae) studied in the Great Western Woodland, Western Australia. Measurements adapted from Johnstone and Storr (2004), and de Reilbera (2006) for adult males and females combined. In all species, males are larger than females, but the differences are too small to sex free-flying birds. Bill shape most readily separates long-billed from short-billed honeyeaters.

| Species                                                  | Average Weight (gms) | Mean Head Bill Length (mm) | Bill Shape |
|----------------------------------------------------------|----------------------|----------------------------|------------|
| <b>LONG-BILLED</b>                                       |                      |                            |            |
| Brown Honeyeater <i>Lichmera indistincta</i>             | 10.6                 | 34.3                       | decurved   |
| Red Wattlebird <i>Anthochaera carunculata</i>            | 106.7                | 62.3                       | decurved   |
| Spiny-Cheeked Honeyeater <i>Acanthagenys rufogularis</i> | 43.3                 | 48.4                       | decurved   |
| White-Fronted Honeyeater <i>Purnella albifrons</i>       | 17.5                 | 38.1                       | decurved   |
| <b>SHORT-BILLED</b>                                      |                      |                            |            |
| Brown-Headed Honeyeater <i>Melithreptus brevirostris</i> | 12.7                 | 29.9                       | straight   |
| White-Eared Honeyeater <i>Lichenostomus leucotis</i>     | 20.2                 | 37.7                       | straight   |
| Yellow-Plumed Honeyeater <i>Lichenostomus ornatus</i>    | 17.8                 | 34.1                       | straight   |
| Yellow-Throated Miner <i>Manorina flavigula</i>          | 56.5                 | 49.8                       | straight   |

long-billed honeyeaters, the Red Wattlebird and Spiny-Cheeked Honeyeater are larger than the Brown and White-fronted Honeyeaters, with the White-fronted Honeyeater larger than the Brown Honeyeater (Table 1). Among the short-billed honeyeaters, the Yellow-throated Miner is the largest and the Brown-headed Honeyeater the smallest. White-eared and Yellow-plumed Honeyeaters are similarly sized.

While observing honeyeaters, we noted behavioural differences among the eight species. Although all species aggregated in mixed flocks at blooms of nectar-rich flowers and moved between patches of flowers in flocks, they differed in social behaviour. Brown Honeyeater, Red Wattlebird, Spiny-cheeked Honeyeater, White-fronted Honeyeater, and White-eared Honeyeater tended to be solitary or pair foragers and were pair territorial when nesting. All species of honeyeaters were aggressive in defending nectar sources, particularly against smaller species and conspecifics. Red Wattlebird was especially aggressive in defending flowering trees or patches of flowering trees. Brown-headed Honeyeater, Yellow-throated Miner, and Yellow-plumed Honeyeater foraged in flocks. Brown-headed Honeyeater is a solitary nester. Yellow-throated Miner formed small flocks, with multiple individuals associated with each nest; that is, they were co-operative nesters. Yellow-plumed Honeyeaters formed large nesting colonies that were defended aggressively against other birds, with the smaller shrub and canopy foragers excluded (HFR unpubl.). It is likely that Brown-headed and Yellow-plumed Honeyeaters also nested co-operatively (HFR pers obs.).

## Methods

### Foraging behaviour

Details of the procedures used to record foraging behaviour are given in Recher and Davis (1998, 2002), but briefly we recorded the species of bird, the substrate and height of the food, the genus or species of plant from which food was taken, and the foraging manoeuvre or method used by the

bird to take food. For substrates and manoeuvres we used the terminology of Recher *et al.* (1985) and Recher and Davis (1998, 2002). Observations commenced shortly after sunrise and depending on weather conditions continued to dusk. We began on a different site each day and minimized recording data on the same individuals by moving between sites, and by choosing different sites on successive days. Foraging was recorded for all birds encountered.

For each individual, we recorded up to five consecutive foraging manoeuvres, including probing for nectar, commencing with the second observed manoeuvre following Recher and Gebski (1989). Only manoeuvres in which the bird obtained or attempted to obtain food were recorded.

Here we combine bark, dead wood, loose bark, and hanging bark as 'bark'; twigs and petioles, and live and dead leaves as 'foliage'; and, bare ground, litter, logs, and coarse woody debris as 'ground'. Some, but not all, observations of ground-foraging may have been confused with birds gathering nest material. For manoeuvres, 'glean flower' and 'probe flower' were combined as 'probe flower', with the taking of nectar distinguished from feeding on arthropods at flowers. Honeyeaters used their brush-tongues to take nectar from flowers in a manoeuvre we described as 'probing', with no distinction between species. The difference between taking arthropods or nectar from flowers was distinguished in two ways; feeding on nectar involved rapid movements of the tongue and prolonged (often deep) probing into the flower, whereas arthropods were taken with the beak, a distinct snap and rapid movement of the head. 'Hover hawk' and 'hover glean' are combined with 'hover'. Rare behaviours (pounce, flush chase, prise/flake, and snap; <0.001% of honeyeater observations) were deleted from analyses.

### Data analysis

#### Foraging substrates and manoeuvres

The difference between long- and short-billed honeyeaters

in the proportion of nectar feeding was tested using a paired sample (correlated) t-test, with each year and location treated as a sample. Chi square was used to test for associations between species and locations in the use of non-nectar foraging substrates and manoeuvres.

### Foraging heights

Observations of foraging for nectar and non-nectar foraging were sorted into 2 m height intervals (i.e., 0–2 m, 2–4 m, ... > 13 m) combining all years and locations and tested for associations between species using Chi square. Small sample sizes for many species precluded doing this for individual locations (see Appendix A for sample sizes).

### Plant species

We tested for associations between species and the species of plants used for nectar foraging at each location using Chi square. Only species with > 80 observations in a location were included in the analyses.

For non-nectar plants we used Chi square to test for associations between long- and short-billed species (species combined) in the mean number of plant species used in each location, treating each year as a sample. Small sample sizes precluded testing for associations between individual species and the plants used for non-nectar foraging.

### Species similarity

The Shannon Index ( $H'$ ) was calculated for each species in each location for non-nectar foraging substrates and manoeuvres. Differences in the Shannon Index between species were then tested for significance using the ‘compare diversities’ procedure under the ‘diversity’ menu in the PAST statistical package.

We used cluster analysis (CA) (based on Bray-Curtis similarities) and principal components analysis (PCA) to identify similarities and differences among species with all locations and years combined. In both instances we tested various combinations of variables including percent use of non-nectar foraging substrates and manoeuvres, percent nectar-feeding, mean body weight, head/bill length, and Shannon indices for non-nectar foraging substrates and foraging manoeuvres. Plant species were not used, as differences in plant species composition would have skewed the analyses to the most frequently sampled locations. For cluster analysis we used percentages of observations. For PCA analyses foraging data were transformed to provide a mean of zero and standard deviation of one for each variable.

As neither CA nor PCA is a statistical procedure to which probabilities can be applied, we selected results which accounted for the highest levels of variance and which seemed to best describe the relationships among species.

### Sample Size

Sample sizes differed among species between locations (Appendix A). Due to small sample sizes for individual species and years, most analyses presented combine observations from all years at each location. In some instances, all observations (locations and years) are

combined to provide an overview of foraging habits for the GWW as a whole. However, differences between locations in plant species prevented this from being done for analyses of use of plant species for nectar- and non-nectar foraging and these data are presented separately for each location. Given the differences in plant species composition and patterns of flowering, observations of the use of plant species were also adjusted for differences between locations and years in the number of person hours of observation.

All statistical analyses were done using the PAST statistical package available from [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm) (Hammer *et al.* 2001, Hammer and Harper 2006).

## Results

### Nectar and Non-nectar foraging

All honeyeaters visited flowers to take nectar. They also fed on lerp, honeydew, and arthropods; we did not observe honeyeaters taking manna or feeding on sap in the GWW. The percent of nectar-feeding differed between species and locations (Table 2). At all locations, with all years combined, more than 63% of observations of long-billed honeyeaters were of birds foraging for nectar (Table 2). Combining all locations and years, 83.5–90.6% of observations of the species of long-billed honeyeaters were of birds feeding on nectar, while for species of short-billed honeyeaters 33.1–58.9% of observations were of nectar-feeding. The differences in mean percent nectarivory for long- vs. short-billed species were significant for Yellow-dine ( $t_6 = 6.61$ ,  $p = 0.0006$ ), Norseman North ( $t_4 = 3.67$ ,  $p = 0.011$ ), Norseman West ( $t_4 = 10.18$ ,  $p < 0.0001$ ), and all locations and years combined ( $t_6 = 9.53$ ,  $p < 0.0001$ ). Results for Widgiemooltha were not significant ( $t_4 = 2.57$ ,  $p = 0.062$ ), but this may be the result of small sample sizes.

### Non-nectar foraging substrates

Honeyeaters took food other than nectar from a wide variety of substrates; foliage, bark, and air, with limited foraging on the ground, flowers (arthropods), and on fruit. In Figure 2, non-nectar foraging observations from all locations and years are combined and use of substrates compared among species. The differences among species are significant ( $\chi^2_{35} = 1800$ ,  $p < 0.001$ ). Brown-headed, Yellow-plumed, and Spiny-cheeked Honeyeaters, and Red Wattlebird foraged predominantly on foliage when not taking nectar. Brown and White-fronted Honeyeaters took most prey from the air, while Yellow-throated Miner and White-eared Honeyeater were mainly bark foragers. Ground-foraging was most frequent by Brown and White-eared Honeyeaters, and Yellow-throated Miner. Despite the high frequency of visiting flowers for nectar, honeyeaters rarely took arthropods from flowers (Figure 2). Native Cherry *Exocarpos apollinus* fruit was a significant part of the non-nectar diet of Spiny-cheeked Honeyeater (28%) at Yellow-dine.

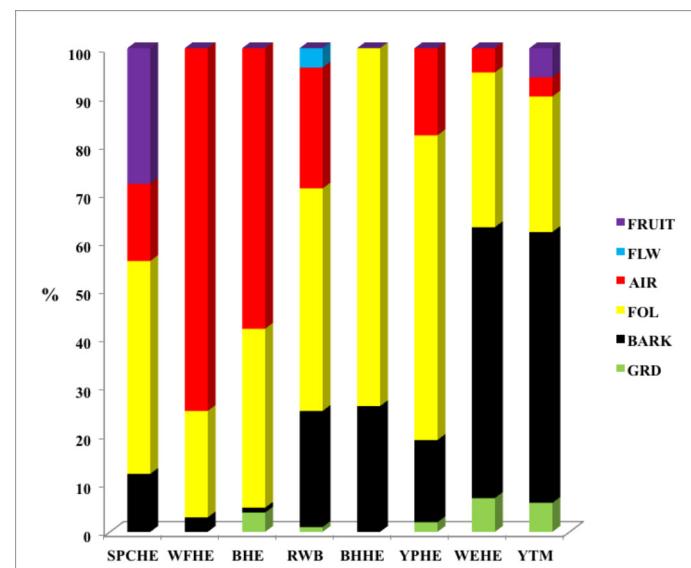
With all years of observation combined and less frequently used substrates (ground, flowers, and fruit) deleted, the use of substrates by different species was associated significantly with location (number of  $\chi^2$  tests = 4,  $p < 0.0001$  for all

**Table 2.** Percent nectar-feeding ( $\pm 95\%$  confidence limits) by nectar-feeders in the eucalypt woodlands of the Great Western Woodland at four locations; Widgiemooltha (WIDGIE), Yellowdine (YELLOW), Norseman North (NORS NTH), Norseman West (NORS WST), and for the four locations combined (All). Data were collected between 1997 and 2010, with data from all years of observation in each area combined after adjusting for differences in person hours of observation/year. Sample sizes at some locations for some species were too small to calculate confidence limits. Spiny-cheeked Honeyeater and Yellow-throated Miner were rare or absent from Norseman North and West. See Table 1 for scientific names.

| Species                  | WIDGIE      | YELLOW      | NORS NTH    | NORS WST    | ALL  |
|--------------------------|-------------|-------------|-------------|-------------|------|
| <b>LONG-BILLED</b>       |             |             |             |             |      |
| Brown Honeyeater         | 63.3        | 93.5 (4.8)  | 91.4 (18.5) | 82.7 (11.5) | 83.5 |
| Red Wattlebird           | 85.1 (3.2)  | 72.6 (11.2) | 87.0 (6.1)  | 85.8 (5.1)  | 84.5 |
| Spiny-cheeked Honeyeater | 98.6        | 83.9 (7.3)  | ND          | ND          | 88.5 |
| White-fronted Honeyeater | 96.6        | 93.1 (5.4)  | 92.5        | 84.4 (15.5) | 90.6 |
| <b>SHORT-BILLED</b>      |             |             |             |             |      |
| Brown-headed Honeyeater  | 52.2 (30.5) | 55.3 (23.7) | 63.9 (26.6) | 59.5 (9.2)  | 58.9 |
| White-eared Honeyeater   | 49.7 (27.1) | 54.7 (4.8)  | 21.1 (12.0) | 22.1 (35.6) | 33.1 |
| Yellow-plumed Honeyeater | 45.1 (22.4) | 55.2 (4.0)  | 55.4 (7.2)  | 40.6 (6.0)  | 46.4 |
| Yellow-throated Miner    | 51.2 (28.4) | 14.6        | ND          | ND          | 44.4 |

tests). At Widgiemooltha, Norseman North, and Norseman West, long-billed honeyeaters hawked insects from the air more frequently than short-billed honeyeaters. Brown-headed Honeyeater was the only species not to take insects from the air in any location. At Yellowdine, the distinction between long-and short-billed species was less pronounced, with foliage and bark the most frequently used substrates by all species except White-fronted and Brown Honeyeaters, which took prey mostly (>95% of foraging observations) from the air or foliage. Spiny-cheeked Honeyeaters foraged extensively on fruit at Yellowdine, but also took prey from foliage, bark, and air. Spiny-cheeked Honeyeater was primarily an aerial forager at Widgiemooltha; they were absent or rare on the Norseman sites. At Widgiemooltha and Norseman North, White-eared Honeyeater foraged mainly on bark substrates, but took more prey from foliage at Yellowdine and Norseman West. In all locations, Red Wattlebird and Yellow-plumed Honeyeater tended to be foraging generalists taking prey frequently from air, foliage, and bark. Yellow-throated Miner foraged mainly on foliage at Yellowdine and on bark at Widgiemooltha; they did not occur on the Norseman sites.

Small insects (often less than 1-2 mm in size) were the principal sized prey taken aerially. Insects and spiders were taken from foliage and bark, but the most frequently observed food from foliage was lerp produced by psyllid insects (Psylidae: Hemiptera). Generally it was not possible to determine if the insect itself or only the lerp was taken. However, observations of honeyeaters at Norseman North that were foraging from the ground on a large glycapsid psyllid on the foliage of eucalypt seedlings found that both the lerp and the psyllid were removed (HFR pers obs). Most foraging on bark was of birds probing under loose and decorticating bark for honeydew, which was taken using the tongue in the same way as taking nectar (HFR pers obs). Honeydew was also taken from hemipterans (e.g., aphids, scale insects) on twigs and small branches.



**Figure 2.** Non-nectar foraging substrates used by honeyeaters in the Great Western Woodland. Foraging data from Yellowdine, Widgiemooltha, Norseman North, and Norseman West and all years (1997-2010) of observation were combined after adjusting for the number person hours of observation. Small sample sizes for many species precluded comparisons by location. Long-billed species are Spiny-cheeked Honeyeater (SPCHE), White-fronted Honeyeater (WFHE), Brown Honeyeater (BHE), and Red Wattlebird (RWB). Short-billed species are Brown-headed (BHHE), Yellow-plumed and White-eared (WEHE) Honeyeaters, and Yellow-throated Miner (YT).

### Manoeuvres

Combining observations from the four locations of the manoeuvres used to take food other than nectar separated species that use more active manoeuvres (e.g., hawk, snatch, hover) from those that take food by gleaning and probing (Figure 3). Insects were hawked from the air, while hovering was used to take insects from the air and

from foliage. Honeydew and arthropods were taken by probing beneath loose and decorticating bark. Brown-headed Honeyeater often probed leaves glued together by insect larvae in a behaviour commonly associated with hang-gleaning. Gleaning, snatching, and hang-gleaning were mainly used to take arthropods and lerp from foliage and bark. For all years and locations combined, excluding foraging for nectar, foraging manoeuvres were significantly associated with species ( $\chi^2_{35} = 1520$ ,  $p < 0.0001$ ).

White-fronted and Brown Honeyeaters took more than half their prey by hawking (Figure 3). Brown Honeyeater hovered more frequently than other species. Red Wattlebird, Yellow-plumed, and Spiny-cheeked Honeyeaters were predominantly gleaners, with Red Wattlebird and Yellow-plumed Honeyeater also hawking. The large proportion of gleaning by Spiny-cheeked Honeyeater reflects its frequent feeding on fruit, which we described as gleaning (Figure 2). White-eared Honeyeater and Yellow-throated Miner probed more frequently than other species, but also gleaned. The Brown-headed Honeyeater was primarily a gleaner, but also hang-gleaned and probed. Hang-gleaning distinguishes the foraging behaviour of Brown-headed Honeyeater from other short-billed honeyeaters.

Probing for arthropods or honeydew under bark was unusual for long-billed honeyeaters. We observed probing under bark most frequently for Red Wattlebird, rarely for Brown Honeyeater, and not for White-fronted and Spiny-cheeked Honeyeaters. Instead, most arthropods were taken by gleaning or hawking, with snatching prey less frequent. Gleaning prey (primarily lerp) from foliage was the most common foraging behaviour after nectar-feeding for short-billed honeyeaters. Probing under loose and decorticating bark was also a common

behaviour. Short-billed honeyeaters rarely hawked or snatched prey, with hawking most frequent with Yellow-plumed Honeyeater often in tandem with a flush-chase behaviour (HFR unpubl.).

The use of foraging manoeuvres by different species was significantly associated with location (number of  $\chi^2$  tests = 4,  $p < 0.0001$  for all tests). White-fronted Honeyeater snatched prey more often at Widgiemooltha and Norseman North than at other locations. They also gleaned more at Widgiemooltha than elsewhere. Brown Honeyeater hawked less and hovered more at Yellowdine than other locations. Red Wattlebird gleaned less at Norseman North and hawked more than other locations. Yellow-plumed Honeyeater used similar foraging behaviours throughout. White-eared Honeyeater probed less and hawked more at Yellowdine, and gleaned more frequently at Norseman West than elsewhere. Yellow-throated Miner gleaned more and probed less at Yellowdine than Widgiemooltha. Brown-headed Honeyeater did less hang-gleaning at Yellowdine than elsewhere.

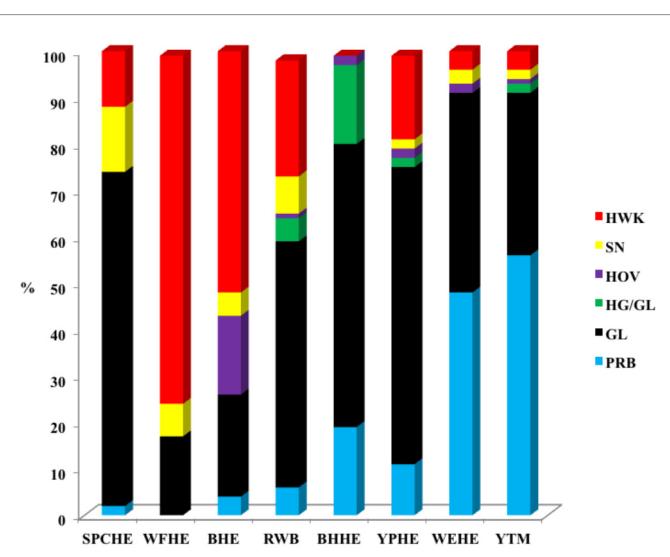
### Foraging heights

The height above the ground at which honeyeaters foraged for nectar and other food broadly overlapped between species (Figure 4). Red Wattlebird and Yellow-plumed Honeyeater foraged higher than other species, although at Norseman West Yellow-plumed Honeyeater took nectar mainly from low-growing mallees. All species foraged over the full height range of available vegetation from the ground to the upper canopy, with foraging heights at each location determined by the foliage profile of the vegetation and differences in habitat selection by species. Brown, Spiny-cheeked, and White-fronted honeyeaters tended to forage lower than other species (Figure 4) reflecting their greater abundance in low woodlands with an extensive shrub layer (HFR unpubl. abundance and habitat data).

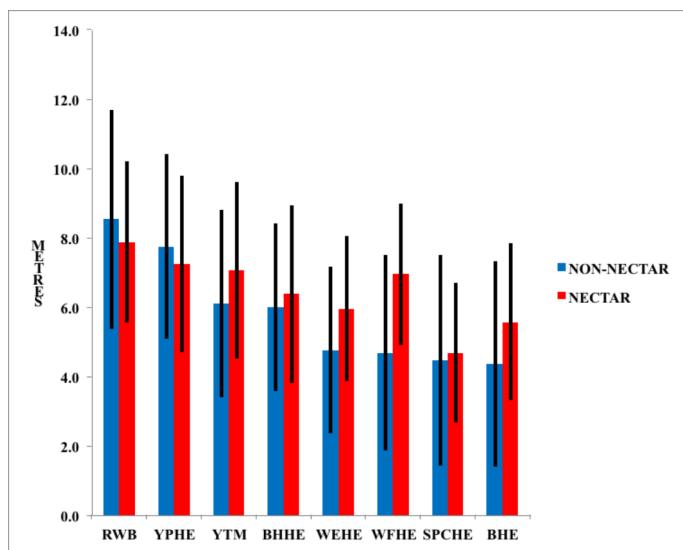
Although foraging heights broadly overlapped, there were significant associations for the GWW as a whole for species and nectar ( $\chi^2_{28} = 979.45$ ,  $p < 0.0001$ ) and non-nectar foraging ( $\chi^2_{28} = 766.42$ ,  $p < 0.0001$ ). When foraging for nectar, there was no significant difference in the foraging heights of Brown and White-eared Honeyeaters ( $\chi^2_4 = 10.833$ ,  $p = 0.03$ ); all other pairs of species differed (number of  $\chi^2$  tests = 27,  $p's < 0.0001$ ). For non-nectar foraging, there was no difference in the foraging height profile of Brown Honeyeater with Spiny-cheeked ( $\chi^2_4 = 5.643$ ,  $p = 0.2$ ) and White-eared ( $\chi^2_4 = 7.163$ ,  $p = 0.1$ ) Honeyeaters. There was also no difference in foraging height profiles between White-fronted and Spiny-cheeked Honeyeaters ( $\chi^2_4 = 10.466$ ,  $p = 0.03$ ). All other pairs of species differed (number of  $\chi^2$  tests = 25,  $p < 0.0001$  for all tests) in the foraging height profiles where non-nectar foods were taken.

### Plant species

Vegetation structure and plant species composition differed between Yellowdine, Widgiemooltha, Norseman North, and Norseman West (HFR unpubl. data). There were also differences in floristic composition and structure between sites in each location. Here we consider the main sources of nectar used by honeyeaters in each location and the plant



**Figure 3.** Manoeuvres used by honeyeaters in the Great Western Woodland to take food other than nectar. Observations of non-nectar foraging were combined for all locations and years after adjusting for the number person hours of observation. Infrequently used behaviours (flush, snap, prise, and pounce; <0.02% of observations), were deleted. Hover, hover-glean, and hover-hawk were combined as 'hover' (HOV). Other manoeuvres are hawk (HWK), snatch (SN), hang-glean (HG/GL), glean (GL), and probe (PRB). Species legend given in Figure 2.



**Figure 4.** Mean and standard deviation of foraging heights of honeyeaters in the Great Western Woodland feeding on nectar and non-nectar foods (e.g., lerp, arthropods). All locations and years have been combined after adjusting for the number person hours of observation. Species are ranked by mean foraging height when taking food other than nectar. Species legend given in Figure 2.

species on which honeyeaters foraged for foods other than nectar. Honeyeaters took nectar and other foods from a wide variety of plant species (Figures 5 and 6).

#### Nectar plants

Eucalypts, (Gimlet, Merrit, Redwood, Red Morrel, Sand Mallee, Square-fruited Mallee, Yorrel, and mallee species) were the primary sources of nectar at Widgiemooltha, Norseman North, and Norseman West (Figure 5). Eucalypts and Poverty Bush (*Eremophila* spp.) were the primary sources of nectar at Yellowdine (Figure 5). Nectar was also obtained from species of mistletoe, *Grevillea*, and other eucalypts (Coral Gum *E. torquata*, Dundas Blackbutt, Goldfields Blackbutt, Ribbon Gum, and Salmon Gum), although during the times and locations where we worked in the GWW these were not abundant sources of nectar. Sources of nectar differed between locations (Figure 5) and years according to what species were in flower and the species composition of the vegetation. The places where we worked had few plants other than eucalypts which provided nectar for honeyeaters (HFR pers obs.).

There were significant associations in all locations between honeyeaters and the species of eucalypts used for nectar (Yellowdine:  $\chi^2_{28} = 761.32$ ,  $p < 0.0001$ ; Widgiemooltha:  $\chi^2_{21} = 335.57$ ,  $p < 0.0001$ ; Norseman North:  $\chi^2_{24} = 1071.5$ ,  $p < 0.0001$ ; Norseman West:  $\chi^2_{35} = 1661.9$ ,  $p < 0.0001$ ). At Yellowdine, Yorrel and mallees were the most important sources of nectar, with Brown-headed Honeyeater most often taking nectar from Gimlet (Figure 5). *Eremophila* was important for miners, and Brown and Spiny-cheeked Honeyeaters. At Widgiemooltha, Merrit and Redwood were the most frequently used nectar sources, with Square-fruited Mallee important for miners, Yellow-plumed, Brown, and Spiny-cheeked Honeyeaters. At Norseman North, Merrit was the principal source of nectar for Brown-headed Honeyeater and Red Wattlebird, with Yellow-plumed

Honeyeater using Merrit and Red Morrel. Sand Mallee and Gimlet, followed by Merrit and Red Morrel were the most frequently used sources of nectar at Norseman West. At Norseman West Red Wattlebirds, Brown-headed and White-eared Honeyeaters most frequently used Gimlet, while Yellow-plumed Honeyeater often took Red Morrel nectar (Figure 5).

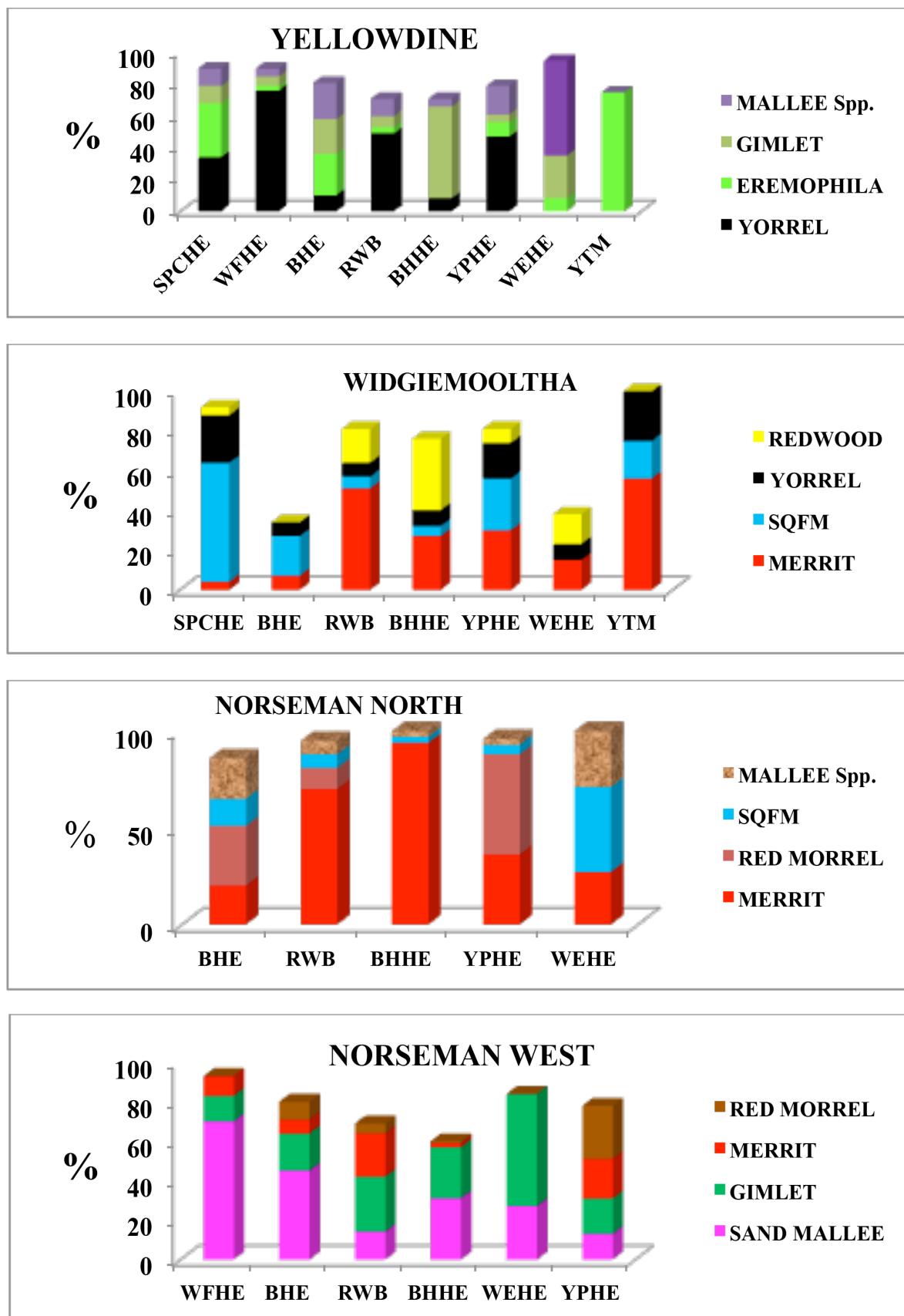
With all locations and years combined, which weights observations to Norseman West, where there were more observations over more years, there is no separation of long-billed and short-billed honeyeaters in their use of eucalypt nectar using PCA or CA. Among the long-billed honeyeaters, Brown Honeyeater took nectar most frequently from Sand Mallee and Red Morrel; White-fronted Honeyeater from Sand Mallee, Merrit, and Yorrel; Red Wattlebird from Merrit and Gimlet; and Spiny-cheeked Honeyeater from Yorrel and Square-fruited Mallee. Among the short-billed honeyeaters, White-eared Honeyeater took nectar most frequently from Gimlet, Square-fruited Mallee, and Merrit; Brown-headed Honeyeater from Merrit and Gimlet; Yellow-plumed Honeyeater from Red Morrel and Merrit; and Yellow-throated Miner from Merrit. Brown and Yellow-plumed Honeyeaters were the only species to use cup-shaped (Red Morrel) flowers frequently, with all other species making greatest use of flowers with long, pendulous flowers, such as Sand Mallee and Merrit.

#### Non-nectar plants

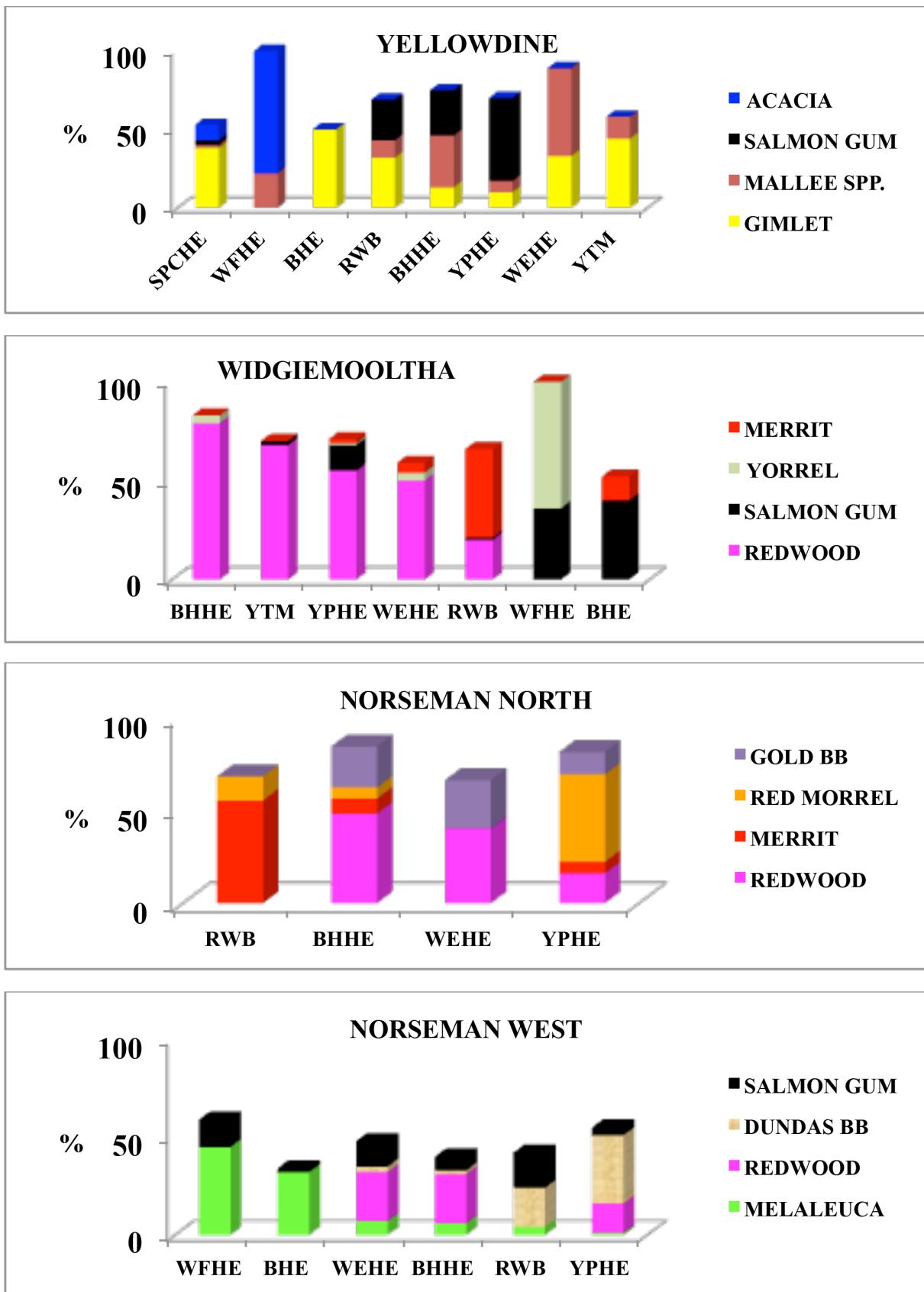
Eucalypts were the plants most frequently used by honeyeaters foraging for arthropods and alternative carbohydrates (i.e., lerp and honeydew) (Figure 6). As with the use of eucalypts for nectar, there were differences between locations in the species of eucalypts used by honeyeaters to take non-nectar foods (Figure 6). Sample sizes for most species of honeyeater taking non-nectar foods were too small to analyse differences among species in the selection of plant species.

Dundas Blackbutt, Gimlet, Goldfields Blackbutt, Merrit, Red Morrel, Redwood, Salmon Gum, Square-fruited Mallee, Yorrell, and mallee species, were the most frequently used eucalypts among the four locations. Native Cherry was an important source of fruit at Yellowdine for Spiny-cheeked Honeyeater and Yellow-throated Miner. Although wattles *Acacia* spp. were abundant in all locations, apart from White-fronted Honeyeater at Yellowdine, few honeyeaters foraged on them. Broom Bush was abundant in all locations, and was visited frequently by honeyeaters foraging for arthropods at Norseman West, but not at other locations. Across all locations (all years combined) long-billed honeyeaters foraged on fewer species (= 4.3 species) of plants than short-billed honeyeaters (= 8.9 species) ( $t_6 = 2.74$ ,  $p = 0.034$ ). The number of species of plants used to forage for arthropods and fruit by long- and short-billed species between locations (all years combined) did not differ ( $\chi^2_3 = 0.6$ ,  $p = 0.9$ ).

Red Wattlebird and Yellow-plumed Honeyeater were the only species to frequently forage in the crowns of emergent trees. Although all honeyeaters took lerp from the foliage of eucalypts, Brown and White-fronted Honeyeaters foraged the least for lerp and more frequently searched



**Figure 5.** Percent of plant species visited by honeyeaters foraging for nectar at four locations in the Great Western Woodland. Only the four most frequently visited plant species at each location are shown. Spiny-cheeked Honeyeater and Yellow-throated Miner did not occur at the Norseman sites. Observations for all years were combined after adjusting for the number person hours of observation. Bird species legend given in Figure 2. SQFM in the plant legend is Square-fruited Mallee.



**Figure 6.** Percent of plant species visited by honeyeaters foraging for food other than nectar at each of four locations in the Great Western Woodland. Only the four most frequently visited plant species are shown. Spiny-cheeked Honeyeater and Yellow-throated Miner did not occur at the Norseman sites, and there were too few non-nectar foraging observations for Brown and White-fronted Honeyeaters at Norseman North to plot. Observations for all years were combined after adjusting for the number person hours of observation. Species legend given in Figure 2. BB in the plant legend is 'Blackbutt'.

for arthropods in *Melaleuca* and *Acacia*. White-eared Honeyeater and Yellow-throated Miner probed loose and decorticating bark for honeydew and arthropods. As a result, they were most likely to forage in mallees, Gimlet, Redwood, and other eucalypts with loose and decorticating bark. Yellow-plumed Honeyeater most often foraged on the foliage and bark of the dominant eucalypts within the area of their colonies. Thus, at Yellowdine Yellow-plumed Honeyeater were most often observed foraging in Salmon Gum and Red Morrel, at Widgiemooltha in Redwood, at Norseman North in Red Morrel, Goldfields Blackbutt, and Redwood, and at Norseman West in Dundas Blackbutt, Red Morrel, and Redwood. Brown-headed Honeyeater and Red Wattlebird occurred in most habitats and appeared to forage indiscriminately in all species of eucalypts according to their abundance. Brown-headed Honeyeater also foraged in a range of shrubs and mallees, including *Melaleuca*, *Persoonia*, *Exocarpos*, *Acacia*, and *Atriplex*.

#### Species similarity

Among the long-billed honeyeaters, Brown Honeyeater and Red Wattlebird used a significantly more diverse array of foraging manoeuvres than Spiny-cheeked and White-fronted Honeyeaters (Table 3). Red Wattlebird and Spiny-cheeked Honeyeater used a significantly more diverse array of foraging substrates than Brown and White-fronted Honeyeaters. There were no differences in the diversity of foraging manoeuvres used by short-billed honeyeaters, but species differed in the diversity of substrates used (Table 3), Brown-headed Honeyeater used a significantly less diverse array of substrates than other short-billed honeyeaters, while Yellow-plumed Honeyeater also differed significantly from Yellow-throated Miner (Table 3). There were no differences in the diversity of substrates used by White-eared Honeyeater and Yellow-throated Miner (Table 3).

Compared with long-billed honeyeaters, the foraging manoeuvres of short-billed honeyeaters were less diverse

than those of Brown Honeyeater and Red Wattlebird, but more diverse than Spiny-cheeked and White-fronted Honeyeaters (Table 3). White-eared and Yellow-plumed Honeyeaters, and Yellow-throated Miner were more diverse in the substrates used than Brown and White-fronted Honeyeaters, but less so than Red Wattlebird and Spiny-cheeked Honeyeater (Table 3).

In a CA using all foraging and morphological variables, the two largest species (Red Wattlebird and Yellow-throated Miner) were separated from the smaller species, with the long-billed Spiny-cheeked, White-fronted, and Brown Honeyeaters separated from the short-billed White-eared, Brown-headed, and Yellow-plumed Honeyeaters. Within each of these clusters, the largest species (Spiny-cheeked and White-eared Honeyeaters) were separated from the smaller species (Bray-Curtis, cophenetic correlation coefficient (coph. corr.) = 0.7259).

Restricting the variables to mean body weight, diversity ( $H'$ ) of non-nectar foraging substrates and manoeuvres, mean nectar and non-nectar foraging heights, and percent nectar foraging provided the 'most satisfying' grouping of species (Bray-Curtis, coph. corr. = 0.8536); long-billed honeyeaters were grouped separately from short-billed honeyeaters (Figure 7). Within each group the largest species were separated from the smaller species. If body weight is replaced by head/bill length, the same clusters are obtained, but with a lower coph. corr. (0.7036). This was a common association of species and did not change with the deletion of percent non-nectar foraging manoeuvres and substrates, and/or diversity ( $H'$ ) values from the analysis.

PCA using all non-nectar foraging substrates, % nectar-feeding (%N), body weight (WGT), and head/bill length (H/B) separated long-billed from short-billed honeyeaters, with 67% of the variance accounted for by the first two components (Figure 8). Component 1 (38.7% of variance) is negatively associated with ground (GR) and bark (BK) foraging and positively with percent feeding on nectar and

**Table 3.** Diversity ( $H'$ ) for the substrates and manoeuvres used by long- and short-billed honeyeaters when foraging for foods other than nectar at Yellowdine, Widgiemooltha, Norseman North, and Norseman West in the Great Western Woodland. Species were tested for significant differences in the diversity of substrates and manoeuvres used. Species are Brown Honeyeater (BHE), Red Wattlebird (RWB), Spiny-cheeked Honeyeater (SPCHE), White-fronted Honeyeater (WFHE), Brown-headed Honeyeater (BHHE), White-eared Honeyeater (WEHE), Yellow-plumed Honeyeater (YPHE), and Yellow-throated Miner (YTM). Observations for all years (1997–2010) were combined, with some rarely used substrates and maneuvers deleted. Letters in the p < .01 column indicate significant differences between species.

| Manoeuvres          |      |             | Substrates |      |             |
|---------------------|------|-------------|------------|------|-------------|
|                     | H'   | p < 0.01    |            | H'   | p < 0.01    |
| <b>Long-billed</b>  |      |             |            |      |             |
| a BHE               | 1.23 | c,d         | BHE        | 0.87 | b,c,e,h     |
| b RWB               | 1.29 | c,d,e,f,g,h | RWB        | 1.22 | a,d,e,f,g   |
| c SPCHE             | 0.84 | a,b         | SPCHE      | 1.27 | a,d,e,f,g   |
| d WFHE              | 0.71 | a,b,e,f,g,h | WFHE       | 0.64 | b,c,f,g,h   |
| <b>Short-billed</b> |      |             |            |      |             |
| e BHHE              | 1.04 | b,d         | BHHE       | 0.60 | a,b,c,f,g,h |
| f WEHE              | 1.03 | b,d         | WEHE       | 1.02 | b,c,d,e     |
| g YPHE              | 1.09 | b,d         | YPHE       | 0.97 | b,c,d,e,h   |
| h YTM               | 1.01 | b,d         | YTM        | 1.14 | a,d,e,g     |

aerial foraging (AI). Component 2 (28.4%) is negatively associated with aerial foraging, and positively associated with body weight (size) and use of fruit (FR). Component 3 (20.2%) is negatively associated with foliage foraging (FO), and positively associated with ground and aerial feeding. Component 4 (11.5%) is positively associated with feeding on fruit. Among the long-billed species, Red Wattlebird is separated by size from Brown and White-fronted Honeyeaters, with further separation of the latter by the frequency of aerial foraging. Size, bark, and ground foraging separate Yellow-throated Miner and White-eared Honeyeater from Yellow-plumed and Brown-headed Honeyeaters, with foliage foraging also distinguishing the latter species. Regardless of the combination of variables used, including non-nectar foraging manoeuvres, the same variables remain the most important in separating long-billed from short-billed species, and separating or grouping species within each of these guilds.

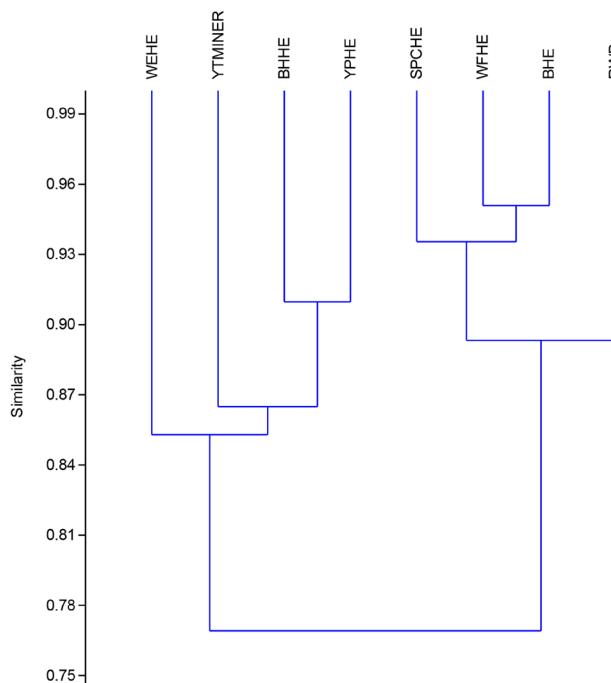
## Discussion

Honeyeaters are among the most abundant birds in the Great Western Woodland (HFR unpubl. data) and multiple species aggregations on nectar-rich flowers are common. Although all species were found together where nectar was abundant, they differed in distribution and

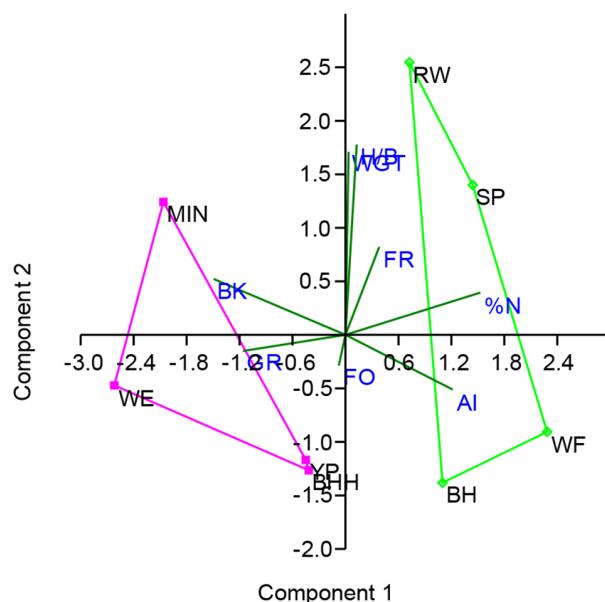
movements in search of food, body size, bill size and shape, foraging behaviour, and social behaviour. These differences segregated species between and within habitats; habitat selection and differences in abundances between years will be considered in subsequent papers. Here we discuss the principal differences in foraging ecology among this group of species all of which require access to energy-rich carbohydrates. The ability of honeyeaters to find and use energy-rich carbohydrates is undoubtedly the reason meliphagids are an abundant and diverse group of birds. This capacity enables them not only to occupy all habitats from desert to rainforest, but allows them to exploit nutrient poor habitats (Recher and Abbott 1970; Recher 1981).

### Long- vs. short-billed honeyeaters

There are two principal foraging guilds of honeyeaters: species with long, decurved bills (e.g., *Acanthagenys*, *Anthochaera*, *Lichmera*, *Myzomela*, *Phylidonyris*), which are primarily nectarivorous, and species with short, straight bills (e.g., *Lichenostomus*, *Manorina*, *Melithreptus*, *Meliphaga*), which rely on alternative carbohydrates (honeydew, lerp, manna, sap) as sources of energy more so than nectar (Keast 1968; Ford and Paton 1977; Halse 1978; Paton 1980; Pyke 1980; Thomas 1980; Recher 1981; Woinarski 1984; Wooller 1984; Mac Nally 1994; Recher and Davis 2011). In the GWW, more than



**Figure 7.** Using mean body weight, diversity ( $H'$ ) of non-nectar foraging substrates and manoeuvres, mean nectar and non-nectar foraging heights, and percent nectar foraging, but excluding percent use of non-nectar foraging manoeuvres and substrates, and head/bill length, long-billed honeyeaters (Spiny-cheeked, White-fronted, and Brown honeyeaters, and Red Wattlebird) are grouped separately from short-billed honeyeaters (White-eared, Brown-headed, and Yellow-plumed Honeyeaters, and Yellow-throated Miner) (Bray-Curtis cluster analysis, Coph. Corr. = 0.8536). Within each group the largest species (Red Wattlebird, Spiny-cheeked Honeyeater, Yellow-throated Miner, and White-eared Honeyeater) are separated from the smaller species. Species legend given in Figure 2.



**Figure 8.** Principal components analysis (PCA) using all non-nectar foraging substrates, percent nectar-feeding (%N), body weight (WGT), and head/bill length (H/B) separated long-billed honeyeaters (Brown Honeyeater [BH], Red Wattlebird [RW], Spiny-cheeked [SP], and White-fronted [WF] Honeyeaters) from short-bill honeyeaters (Brown-headed [BHH], White-eared [WE], and Yellow-plumed [YP] Honeyeaters, and Yellow-throated Miner [MIN]). Within each grouping, species are separated by percent nectar-feeding, size (body weight (WGT)), and head/bill length (H/B), and foraging substrates (bark (BK), ground (GR), air (AI), fruit (FR)).

80% of observations of long-billed species were of birds taking nectar, while less than 60% of observations of short-billed species were of nectar feeding. Comparable differences in the use of nectar by long- and short-billed honeyeaters were found by Ford and Paton (1977) in South Australian eucalypt woodlands and Halse (1978) working in Western Australian heathlands.

The division of honeyeaters into long- and short-billed species in the GWW was supported by cluster and principal components analyses. Both segregated species on the basis of percent nectar feeding and body size, with long-billed honeyeaters forming one group and short-billed honeyeaters a second group. Within each group, the largest species were separated from the smaller species, with further separation based on foraging substrates. Bill length and shape are also factors in separating species (Pyke 1980; Wooller 1984), but our analyses did not consider shape and we did not adjust length to body size. As a result, in our analyses, bill length, as measured by head/bill length, contributed little to the separation of species.

Differences in foraging between long- and short-billed honeyeaters when foraging for lerp, honeydew, and arthropods are also linked to body size and bill morphology. Small size, as in the case of Brown Honeyeater, allows them to forage by hovering, a behaviour rarely seen in larger species (Pyke 1980), but was frequent with Brown Honeyeater in the GWW.

Hang-gleaning by Brown-headed Honeyeater is also consistent with their small size. Honeyeaters with long, decurved bills presumably find gleaning foliage for lerp or arthropods inefficient (Wooller 1984) and obtain the protein they require by hawking insects from the air, an energetically expensive behaviour made possible by the abundance of nectar and other energy-rich carbohydrates available to these birds (Recher and Abbott 1970; Recher 1981). The gleaning behaviour of Spiny-cheeked Honeyeater was mainly in taking fruit.

Bark probing for honeydew and arthropods was a frequent behaviour of White-eared and Brown-headed Honeyeaters, and Yellow-throated Miner. Bark probing was less frequent among Yellow-plumed Honeyeater, but Wilson and Recher (2001) showed that Yellow-plumed Honeyeater often forage almost exclusively from bark. Wilson and Recher (2001) related changes in the use of substrates by Yellow-plumed Honeyeater to seasonal and annual changes in the distribution, abundance and type of foods available. It is likely that many of the differences we recorded between locations and years in the foraging behaviour of honeyeaters in the GWW were the result of annual and local differences in food resources, such as lerp and honeydew, in addition to differences in nectar availability.

Thomas (1980) investigated the foraging ecology of five species of honeyeaters in sclerophyll forest in Tasmania finding that foraging habits varied through the year. As a result, Thomas concluded that the results of short-term or local studies should not be applied to populations as a whole. The studies reported in this paper were conducted at four locations each differing in the structure and composition of the vegetation and honeyeater

assemblages. However, the observations reported were made during spring and it is likely that species differ seasonally and between years in the ways they forage as reported by Thomas (1980) and Wilson and Recher (2001). Further research on the ecology of honeyeaters in the GWW is required to determine the full range of resources used during and between years. Particularly important are studies documenting the movements and flocking behaviour of species as they move between different habitats aggregating where nectar-rich flowers or alternative carbohydrates (e.g., lerp) are abundant.

### Selection of plant species

Most studies of co-habiting honeyeaters found that different species selected different species or genera of plants when nectar-feeding (Keast and Condon 1968; Recher and Abbott 1970; Ford and Paton 1977; Ford 1979; Recher and Davis 2011). These differences are related to body size and bill morphology, as well as differences in size, shape, and amount of nectar between different kinds of flowers (Pyke 1980). Honeyeaters also select flowers by size and sturdiness of available perches, with the largest honeyeaters tending to feed on large inflorescences (e.g., Banksia, Dryandra, Eucalyptus), while smaller species are able to use smaller flowers supported on spindly branches, including those with a long, tubular corolla (e.g., Adenanthos, Epacris, Eremophila) (Ford and Paton 1977; Ford 1979; Pyke 1980; Recher and Davis 2011). Flower size and the sturdiness of available perches were not factors that we observed as important in the GWW where virtually all nectar foraging was on eucalypts, which are sturdy and have similar sized flowers.

The primary nectar sources in the GWW were eucalypts with long, pendulous flowers (e.g., Gimlet, Redwood, Sand Mallee, and Yorrell). Dundas Blackbutt, Goldfields Blackbutt, and Salmon Gum, which flowered sparsely during our studies, as well as several species of mallee and Red Morrel, which flowered more abundantly, had cup shaped flowers. All honeyeaters visited eucalypts with long, pendulous flowers and we only observed large, mixed species aggregations of nectar-feeders on these eucalypts. These were the principal sources of nectar for long-billed honeyeaters, while short-billed honeyeaters frequently took nectar from cup-shaped flowers (e.g., Red Morrel, Salmon Gum).

Although we recorded differences among honeyeaters at each location in the plants selected for nectar-feeding, differences in the choice of nectar plants most likely reflected availability, which in turn reflected habitat differences among the various species of honeyeaters. For example, on the Norseman sites, Yellow-plumed Honeyeater foraged more frequently on Red Morrel blossom than other honeyeaters. This is best explained by the abundance of Yellow-plumed Honeyeater on sites dominated by Red Morrel from which they excluded most other honeyeaters (Recher unpubl.). When nectar-feeding observations are combined for all years and locations there is no difference among honeyeaters in their selection of nectar plants.

As with nectar-feeding, the selection and frequency of use of different plant species and eucalypts when foraging for foods other than nectar appeared to be determined

primarily by plant species abundance, habitat selection, bark structure, species foraging behaviour, and possibly the height of crowns. There were few differences in the foraging heights of honeyeater feeding on nectar or non-nectar foods. Foraging heights were determined by the heights of flowering eucalypts and by vegetation heights where the various honeyeater species were most abundant.

### Opportunistic honeyeaters

In a sense, the honeyeaters we studied in the GWW were generalists responding opportunistically to the availability of nectar, fruit, and other energy-rich carbohydrates. Although the species differed morphologically and had different foraging behaviours, they all showed a capacity to use a wide range of foraging methods and to take food from all available substrates foraging over the entire height range of the vegetation. All required a source of energy-rich carbohydrates and all required arthropods as a source of protein. The allocation of resources among species was therefore complex and differed between locations according to the resources available (e.g., species of eucalypts in flower). Although not presented in this paper, the resources available also differed between years, with honeyeaters changing their behaviour accordingly.

### Conservation and management

In Australia, the conservation and management of highly dispersive species, such as nectar-feeders, is an important conservation issue at a continental scale for which there are few data (Soulé *et al.* 2004; Gilmore *et al.* 2007; Recher 2007). Ford (2013) conservatively estimated that more than half of Australia's land bird species are partially or entirely nomadic or migratory. Recher *et al.* (2010) estimated that more than 60% of the bird species in the GWW were migratory or nomadic, including all species of honeyeaters, with the possible exception of the White-eared Honeyeater. While few of these are currently considered threatened

(Garnett *et al.* 2011), almost all dispersive species in southern Australia have experienced significant losses and degradation of habitat (Saunders and Ingram 1995; Recher 1999; Ford 2011, 2013; HFR unpubl. data). They would be considered threatened if the listing of threatened species were 'proactive', not 'reactive' as currently practised.

The long-term survival of the majority of bird species in Australia is unlikely without significant changes in community and government attitudes towards and understanding of biodiversity conservation. The current paradigm of nature conservation relies almost entirely on the reservation of land as conservation reserves. Conservation reserves are important for nature conservation, but the reserve system in Australia is fragmented and unrepresentative with almost all reserves too small and isolated to ensure the long-term survival of their biota, especially with the advent of a rapidly changing climate accompanied by more frequent and intense fires. The fragmentation of the reserve system coupled with the small size and unrepresentative nature of conservation areas poses immediate threats to migratory and nomadic birds. For these species, a reserve system must not only provide breeding and wintering areas (often widely separated), but there must be continuity of habitat between reserves. For food nomads the requirements are more complex as required food resources shift in space and time with changing weather patterns, season, and from year to year (Collins and Newland 1986; Ramsey 1989; Mac Nally and McGoldrick 1997; McGoldrick and Mac Nally 1998).

It is unlikely that any system of isolated reserves can provide the resources required by migrants and nomads on a sustained basis. This is especially so given, as Ford (2013) emphasized, the lack of detailed information on the movements of nomadic and migratory species or even their basic biology. In the case of the GWW, which was the focus of this paper, the conservation of honeyeaters, along with all other migratory and nomadic species, requires the entire region to be managed as a single functioning ecosystem.

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## APPENDIXND

Number of foraging observations (nectar and non-nectar), all years combined. Scientific names in Table I.

| Years Of Observation            | Yellowdine  | Widgiemooltha | Norseman North | Norseman West | Species' Total |
|---------------------------------|-------------|---------------|----------------|---------------|----------------|
|                                 | 1997-2010   | 2005-2007     | 2006-2010      | 2003-2010     | 1997-2010      |
| <b>SPECIES</b>                  |             |               |                |               |                |
| <b>LONG-BILLED HONEYEATERS</b>  |             |               |                |               |                |
| Brown Honeyeater                | 77          | 79            | 139            | 376           | 671            |
| Red Wattlebird                  | 262         | 536           | 278            | 1601          | 2677           |
| Spiny-cheeked Honeyeater        | 342         | 142           | 5              | 5             | 494            |
| White-fronted Honeyeater        | 145         | 196           | 134            | 320           | 795            |
| <b>SHORT-BILLED HONEYEATERS</b> |             |               |                |               |                |
| Brown-headed Honeyeater         | 161         | 230           | 374            | 555           | 1320           |
| White-eared Honeyeater          | 53          | 159           | 190            | 135           | 537            |
| Yellow-plumed Honeyeater        | 972         | 1790          | 1064           | 2781          | 6607           |
| Yellow-throated Miner           | 55          | 242           | 0              | 0             | 297            |
| <b>TOTAL BY LOCATION</b>        | <b>2067</b> | <b>3374</b>   | <b>2184</b>    | <b>5773</b>   | <b>13398</b>   |

